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STUDIES ON THE DEVELOPMENT OF THE BROODS OF *BOMBUS DIVERSUS* SMITH (Hymenoptera, Apidae)

II. Brood development and feeding habits

By Eisuke Katayama

1780–32, Shimoishigami, Ōtawara City, Tochigi Pref.

In the previous paper (1965), the writer reported the egg-laying habits and related accounts of *Bombus* (*Diversobombus*) *diversus* Smith. In the present paper, the observations on the brood development are dealt together with some notes on the feeding habits.

The colonies observed (A, B, C,) are the same to those described previously. The method employed also does not essentially differ from that given in the previous paper.

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Results and Discussions

1) Duration of egg stage

As shown in Table 1, the duration of egg stage was 4 to 5 days in colony B and 4 to 8 days, mostly 4 to 6 days in colony C (cf. Table 2). As the daylong continuous observation was impossible to be carried out, the duration of egg stage could not be exactly determined except for the following instance.

(Colony A, 1959): The eggs laid on Aug. 18 at 12 h. 50 min. hatched out on Aug. 23 at 6 h. 15 min.

Table 1. *Developmental period of* Bombus diversus *Smith in colony B (in 1963).*

Symbol for brood cell	Date of				Duration of each stage (in days)			
	oviposition	hatching out	cocoon spinning	emergence	egg	larva	pupa	total
A	—	22-vii	30-vii	10-viii	—	8	11	—
B	—	25-vii	2-viii	12-viii	—	8	10	—
C	25-vii	30-vii	6-viii	17-viii	5	7	10	22
D	29-vii	2-viii	10-viii	20-viii	4	8	10	22
E	1-viii	6-viii	—	—	5	—	—	—
F	—	8-viii	15-viii	26-viii	—	7	11	—
G	8-viii	12-viii	19-viii	30-viii	4	7	11	22
H	11-viii	15-viii	23-viii	4-ix	4	8	12	24
I	12-viii	17-viii	26-viii	—	5	9	—	—
J	16-viii	21-viii	28-viii	—	5	7	—	—

The average duration of egg stage would probably be 4.5 to 5 days at the middle of summer. But as these colonies were artificially reared in wooden hives, it is conceivable that environmental conditions were not always optimal to the development, resulting in the fluctuation of the duration of egg stage from 4 to 8 days. According to Brian (1951), the duration of egg stage of *B.* (*Agrobombus*) *agrorum* Fabricius lasted 4 to 6 days, the duration similar to that in *B. diversus*.

Table 2. *Duration of each developmental stage of* Bombus diversus *Smith in colony C (1964).*

Brood cell number	Date of				Duration of each stage (in days)				Number of cocoons and sex of adult bees emerged
	oviposition	hatching out	cocoon spinning	emergence	egg	larva	pupa	total	
4	—	—	29-v	9-vi	—	—	11	—	6 ♀♀
5	20-v	26-v	4-vi	14-vi	6	9	10	25	5 ♀♀
7	31-v	5-vi	11-vi	22-vi	5	6	11	22	7 ♀♀
8	5-vi	9-vi	15-vi	25-vi	4	6	10	20	12 ♀♀
9	9-vi	14-vi	23-vi	3-vii	5	9	10	24	8 ♀♀
10	12-vi	17-vi	24-vi	5-vii	5	7	11	23	6 ♀♀
11	15-vi	21-vi	27-vi	9-vii	6	6	12	24	5 ♀♀
12	22-vi	26-vi	3-vii	14-vii	4	7	11	22	8 ♀♀
13	25-vi	30-vi	7-vii	18-vii	5	7	11	23	11 ♀♀
14	1-vii	5-vii	13-vii	24-vii	4	8	11	23	7 ♀♀
15	3-vii	8-vii	16-vii	26-vii	5	8	10	23	9 ♀♀
16	8-vii	13-vii	20-vii	31-vii	5	7	11	23	8 ♀♀
17	13-vii	18-vii	24-vii	4-viii	5	6	11	22	9 ♀♀
18	18-vii	22-vii	28-vii	8-viii	4	6	11	21	6 ♀♀
19	21-vii	25-vii	31-vii	11-viii	4	6	11	21	10 ♀♀
20	23-vii	28-vii	3-viii	14-viii	5	6	11	22	9 ♀♀
21	26-vii	30-vii	5-viii	15-viii	4	7	10	20	8 ♀♀
22	29-vii	2-viii	9-viii	19-viii	4	7	10	21	10 ♀♀
24	2-viii	6-viii	13-viii	24-viii	4	7	11	22	11 ♀♀
25	4-viii	8-viii	15-viii	25-viii	4	7	10	24	14 ♀♀
26	5-viii	9-viii	16-viii	28-viii	4	7	12	23	9 ♀♀
27	8-viii	12-viii	19-viii	1-ix	4	7	13	24	8 ♀♀
28	9-viii	13-viii	20-viii	2-ix	4	7	13	24	7 ♀♀
30	12-viii	16-viii	24-viii	6-ix	4	8	13	25	10 ♀♀
31	13-viii	17-viii	25-viii	10-ix	4	8	16	28	12 ♀♀
34	16-viii	20-viii	29-viii	12-ix	4	9	14	27	10 ♀♀
35	17-viii	22-viii	1-ix	—	5	10	—	—	9 (♀♀)
42	25-viii	2-ix	—	—	8	—	—	—	—
43	25-viii	2-ix	—	—	8	—	—	—	—
46	31-viii	7-ix	15-ix	24-ix	7	8	9	24	5 ♀♀
47	5-ix	12-ix	18-ix	30-ix	7	6	12	25	8 ♀♀
48	9-ix	15-ix	21-ix	5-x	6	6	14	26	6 ♀♀
49	10-ix	16-ix	22-ix	4-x	6	6	12	24	9 ♂♂
50	12-ix	17-ix	24-ix	6-x	5	7	12	24	6 ♂♂
51	12-ix	18-ix	25-ix	7-x	6	7	12	25	7 ♂♂
52	14-ix	19-ix	27-ix	12-x	5	8	15	28	4 ♂♂
53	15-ix	20-ix	27-ix	16-x	5	7	19	31	8 ♂♂
54	15-ix	20-ix	29-ix	16-x	5	9	17	31	7 ♂♂
56	16-ix	21-ix	2-x	18-x	5	11	16	32	5 ♂♂
57	17-ix	22-ix	2-x	20-x	5	10	18	33	6 ♂♂

(Brood cells Nos. 6, 23, 29, 32–33, 36–41, 44–45, 55 and 58–71 are omitted as they did not develop to pupa or adult.)

The duration of egg stage in colony C lasted 4 to 6 days in the period from late May to middle July, 4 days from middle July to middle August, and 5 to 8 days after late August (Table 2). From the relation between duration of egg stage and average air temperature shown in Fig. 1, it is clear that the duration is greatly affected by temperature. But it is uncertain whether the duration of egg stage in the period Aug. 20~Sept. 10 was affected by temperature alone. In this period, the activities of both foragers and house bees were affected by incessant rains.

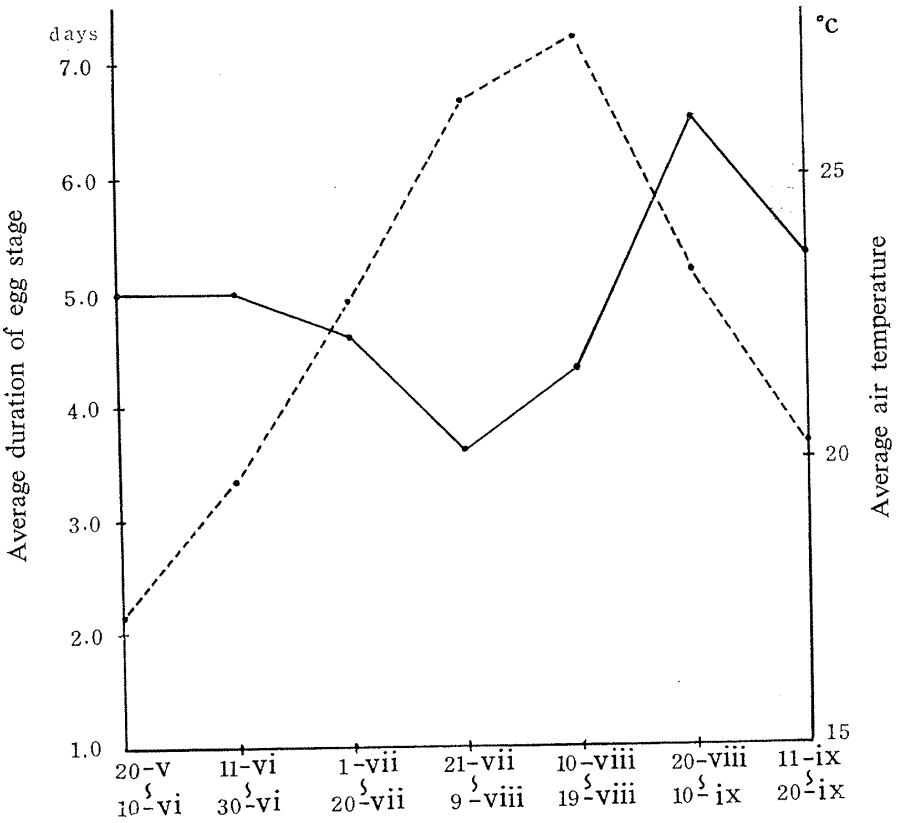


Fig 1. Average duration of egg stage (a solid line) in colony C and average air temperature (a dotted line) at Yaita City in 1964.

2) Hatching out and construction of pollen pocket

As soon as a batch of eggs is laid in an egg-cell, the mouth of the cell is completely sealed with wax. Hence the development of the eggs cannot be observed from the outside of the cell. But worker bumblebees continually manipulate the cell and open the wax wall with their mandibles to examine the eggs. As soon as the workers find the larvae have already hatched out they construct a semicylindrical waxen pouch or pocket on the lower part of one side of the egg-cell to deposit the pollen mass (Plate 1, Fig. a). As shown in Table 3 the diameter of the pocket was generally 6 to 7 mm at the beginning of it, but the pocket attached on

Table 3. *Transition of pollen pocket (diameter in mm) in colony C.*

Brood cell number \ Days after hatching out	Just after hatching out	1	2	3	4	5	6	7
15	6.1	—	8.0	7.7	7.2	8.6	7.5	removed
16	6.0	7.8	8.4 7.8	8.8 7.6	— —	8.2 11.8	— —	〃 〃
17	7.1	—	6.9	8.1 6.4	7.2 6.8	8.2 7.0	removed 〃	
18	6.7	7.3	7.8	6.5 8.6	7.7 removed	7.5	〃	
19	7.2	7.9 7.2	7.8 7.2	8.2 8.2	— removed	—	removed	
20	6.8	9.0	8.7 8.0	7.0 7.0 6.8	8.2 removed 8.0	removed removed		
21	6.2	7.9	9.1 7.7	10.6 7.0	7.7 removed	〃		
22	8.5	7.7	7.8	—	—	removed		
24	—	8.3	7.9	7.1	7.8 9.2	〃 —	removed	
25	—	8.0 7.7	removed 7.9	9.0	8.2	7.4	removed	
26	—	7.9	8.6	10.3	7.5} 7.4} 13.6	8.8 7.6	9.6 8.4	removed 7.5
27	7.1	8.2	7.1 5.1	7.1 6.8	7.2 7.1	8.0 7.4	7.6 7.7	removed 〃
28	—	7.4 Egg cell	7.6 Egg cell	Egg cell 7.1	removed 9.2	9.3	removed	
30	—	7.2	7.2 5.8	8.8 7.6	7.4 7.1	removed 7.1	removed	
31	—	7.3	8.0 6.8	7.3 7.0	7.3 6.8	8.0 7.0	〃 —	removed

the cell No. 22 was 8.5 mm even on the day of hatching out. The height of the pocket seldom exceeds that of the cell to which it is attached.

3) Brood development (Plate 1, Figs. a–f)

After hatching out, the larvae (5–14 per cell) still dwell gregariously in the cell. In general the larval cells are 5 to 6.5 mm in diameter immediately after hatching out (Table 4), and the coloration of the cell wall becomes paler than that of the egg-cell, caused by the gradual decrease of the thickness of wall. The larvae develop very rapidly and usually in about 3 days after hatching out the position of each larva within the cell is detectable from the outside of the cell by the swelling of waxen wall. Within about 4 days after hatching out the larval cell takes the shape of a bunch of grapes and the diameter of each swelling in which the larva lies reaches 9 mm (Plate 1, Fig. e). At this period, the thin silken layer spun by each larva is already detectable under the wax wall. The larvae separate themselves from one another by this silken layer. Tsuneki (1960) also mentioned the separation of larvae by this silken layer in *B. diversus* and *B. (Bombus) ignitus* Smith at the middle to old larval cells. Free & Butler (1959) also mentioned that the larvae of the pocket making species spun flimsy silken partitions between themselves when they were about 5 days old. On 5 days after hatching out, the diameter of the larval cell reaches about 24 mm and the color of the cell becomes brownish yellow. The larvae inside the cell spin silk and line the thin cell wall to make cocoon.

The coloration of the brood cell is dark brown immediately after hatching out but becomes paler as time goes on, brown to brownish yellow after 3 days after hatching out and finally almost yellow immediately before cocoon spinning.

Table 4. *The change of the diameter (in mm) of brood cells in colony C in 1964.*

Brood cell number \ Days after hatching out	Just after hatching out	1	2	3	4	5	6	7
15	6.0	—	9.1	10.5	13.8	15.1	23.4	cocoon spinning
16	4.9	10.1	13.2	18.6	—	27.3	—	finished spinning
17	6.3	—	10.1	13.8	19.7	25.8	finished spinning	
18	6.2	8.9	13.5	17.0	24.6	cocoon spinning	〃	
19	—	9.4	14.8	19.3	23.9	27.4	〃	
20	4.7	8.1	11.8	18.6	23.6	cocoon spinning	〃	
21	5.8	8.1	14.9	17.7	23.8	〃	〃	
22	—	6.9	12.2	16.4	—	—	cocoon spinning	finished spinning
24	—	8.3	11.6	15.2	22.3	26.7	〃	〃
25	—	7.4	13.0	16.0	20.1	25.2	〃	〃
26	—	6.8	10.3	13.6	16.1	21.2	25.8	cocoon spinning
27	6.1	7.6	11.6	12.0	15.1	18.5	22.3	〃
28	—	6.5	8.3	12.1	15.6	18.6	21.8	〃
30	—	6.8	9·1	11.8	14.7	19.2	—	〃
31	6.1	8.0	12.1	—	17.3	20.1	27.4	〃
34	—	6.8	9.1	13.0	15.4	19.6	20.1	—

4) Transition of pollen pocket

In the colonies observed it was rather rare that each cell was provided with only one pollen pocket and usually each cell had 2 pockets. In general a single pocket is attached immediately after hatching out, then about 2 days later 2nd pocket is added (Table 3). The location of the 2nd pocket to that of the 1st one has no definite relation. Two pockets can be made either at the opposite sides of the cell or side by side at the same side.

As shown in Table 3, the diameter of the pocket tends to increase at the earlier larval stage, although the increase is very irregular. In brood cell No. 22, 3 pockets were constructed on a cell, being a relatively rare instance. Toward 4 days after hatching out, the pollen pocket gradually sinks to the base of brood cell according to the increase of the size of the cell. When the cell develops very rapidly, the pocket begins to be removed earlier. In such case the foragers often continue to deposit the pollen pellets into the pocket, which is already vestigial, only remaining at the base of the cell.

Some exceptions as to the pollen pocket were observed as follows: The 2nd pocket of cell No. 18 was constructed at the opposite side of 1st one on July 24 at night and removed already by the daytime on July 26. While 2 pockets of cell No. 26, made side by side in closer contact were fused into a single one with 13.6 mm in diameter 4 days after hatching out. The 1st pocket of cell No. 28 was used twice in place of egg-cell (Aug. 14 and Aug. 15).

In general the pocket retains its perfect form till about 5 days after hatching out. The pollen mass deposited into the pocket is fully consumed by the larvae before about 5 days' elapse after hatching out, but the foragers continue to deposit the pollen as long as the pocket is remaining. Such pollen is consumed not by larvae but by adult bees when they remove the pocket completely.

5) Cocoon spinning

It is difficult to determine the time of the cocoon spinning exactly. Generally speaking however, the larvae begin to spin cocoons on 5 days after hatching out, when they develop rapidly. In the early stage of cocoon spinning, the larvae in the cell can be seen through the thin silken layer in the work of cocooning by moving actively their heads. Adult bees scratch off the waxen cover of the cell with their mandibles little by little as the silken layer inside the waxen cover grows. At this stage, the cocoons are yellowish white. Its silken layer, through which the larvae are still visible, is so thin that easily broken when the adult bees put their legs on it. The duration of cocoon spinning is relatively constant, mostly about a day both in spring and summer, never lasting more than 2 days.

The cocoons just completed are bright to sulfur yellow with dark brown spots of wax not scratched off. The cocoons which developed from the same one egg-cell do not separate, forming a compact mass.

6) Emergence of adult bees

Once completed, the cocoons do not change its external appearance except for the coloration which becomes darker and darker. Immediately before the emergence, on about 9 days after cocoon spinning in spring while on about 8 days in summer, the cocoons become quite dark. The color change is partly caused by the darkening of silk layer itself, but mainly by the advanced pigmentation of the pupa involved.

In most cases adult bees begin to emerge on 9 days after cocoon spinning. In brood cell No. 7 however, the emergence appeared on only 8 days after cocoon spinning. The emergence from the same cocoon group is relatively synchronous. In most cases, all adult bees from the same egg-cell emerge within 3 days. In general the most frequent date of the emergence falls on the 10th to 11th day after cocoon spinning. The duration of emergence was very long in brood cell No. 3, taking 9 days (from June 1 to June 9) for 6 adult bees.

On emergence, the adult bees gnaw the wall of the cocoon with their mandibles from the inside. The older sisters in the nest usually help to make the way out of the cocoon. One instance in colony C (observed June 18 in 1964) is as follows:

One worker bee began to emerge from brood cell No. 13 at 15 h. 21 min. and gnawed the wall of the cocoon with mandibles from the inside. Two adult bees helped to make the way out by gnawing the top of the cocoon. The whole process took about 6 min. Immediately after the emergence the young bee took the honey of a storage pot then went to nesting materials near the comb and emitted excretions there. Returning to the comb, she cleaned herself, then rested for a moment.

7) Total duration of brood development

From the above description and the data given in Tables 1 and 2 the duration of brood development is given as follows:

The duration of egg stage was already mentioned above. The duration of larval stage that is the duration from hatching out to cocoon spinning (the prepupal stage is not included) lasted 7 to 9 days in colony B (observed in 1963), while 6 to 9 days, mostly 6 to 8 days in colony C (observed in 1964). In colony C the duration lasted for about 6 days in the middle of summer from the latter part of July to early in August, while 7 to 9 days in the beginning of summer from the latter part of May to early in June.

The duration of pupal stage, that is the duration from the completion of cocoon spinning to the day of the maximal emergence (= the day when most adult bees emerged from the group of cocoons) lasted 10 to 12 days, mostly for 10 to 11 days both in colonies B and C. In general the duration in colony C lasted 10 to 11 days in earlier phase of the colony. Therefore, the total duration of the development (= the duration from the oviposition to the most frequent day of the emergence) lasted 22 to 24 days in colony B, 20 to 25 days, mostly 22 to 24 days in colony C.

8) Feeding habits

In the colonies observed, no provisioning into the egg-cells was observed at oviposition. As mentioned above the pollen pocket is constructed on the outside of the brood cell soon after the hatching out of larvae, and the food was provided to larvae through this pocket. Foragers returning to the nest with pollen pellets deposit their food into the pollen pocket. At first the forager inserts her anntenae into pollen pocket and examines the inside of it. "If she took a fancy for this pocket" she turns round and inserts her hind legs into the pocket and standing on a pair of fore legs, she scratches pollen pellets off, using middle legs, attaching to the hind tibiae. The pollen pellets deposited into the pocket were kneaded with nectar and plastered to the pollen bed beneath the larvae by the house bees. The foragers usually do not perform this task but leave the pocket into which they deposited pollen pellets, and they left the nest for the next foraging trip. Thus the pollen

pellets are successively deposited into the pocket by foragers and plastered to the pollen bed by house bees.

The larvae do not form a compact mass within the brood cell. Each lies on the pollen bed and eats the latter (Fig. 2). Deposition of the pollen pellets begins soon after the construction of pocket. The foragers continue to deposit the pollen pellets into the pocket until cocoon spinning as long as the pocket remains. The larvae consume the pollen mass in the pocket until about 5 days after hatching out. Thereafter the pollen remaining in the pocket is taken by the adult bees. When the adult bees remove the pocket, they creep under the brood cell and eat the pollen by scratching them off with their mandibles for a long time. After the pollen mass was mostly consumed, there appears a concavity below the group of cocoons developed from one batch of eggs. Small brownish patches of pollen are seen on some parts of this concavity, representing the remains of the previous pollen mass.

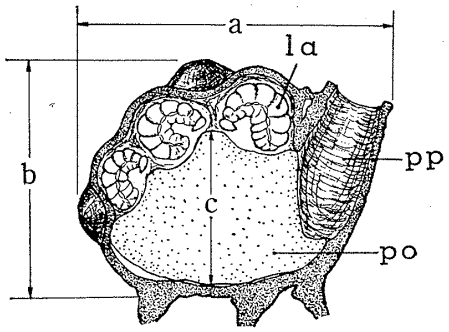


Fig. 2. Longitudinal section of brood cell No. 23. la: larva, po: pollen bed, pp: pollen pocket. a=21.2 mm, b=16.8 mm, c=11.2 mm.

In addition to the feeding through the pocket, this pocket making species feeds occasionally their larvae by the direct regurgitation. In such instance the adult workers make a small hole in the wax wall of brood cells with their mandibles and like as in pollen storing species regurgitate yellowish white milky liquid to the larvae in the cells through this hole. Some instances in colony C (observed in 1964) are cited as follows:

Date	Cell no.	Age of larvae after hatching out	Times of observation
July 5	13	5 days	1
〃 12	15	4	1
〃 13	15	5	1
〃 23	17	5	2
Aug. 1	20	4	1
〃 2	21	3	1
〃 7	22	5	1

In general the regurgitation is made to the middle stage or old larvae of 4–5 days old, never to the larvae in younger than 3 days old. At the tops of cells including 5 days old larvae, which receive regurgitation most frequently, the silken layer is thinner while the waxen wall thicker than the other parts of the cells. On regurgitation, a small hole of 2.1–2.8 mm in diameter is made on the top of the cell. In this species the hole is immediately closed after regurgitation, while it is usually left open in *B. ignitus*. Free & Butler (1959) assumed that the larvae of pocket making species might occasionally be fed with pollen directly regurgitated into their cells by the workers. The present observation on *B. diversus* shows the validity of their assumption. In brood cells Nos. 49–60 (cf. Table 2) containing male larvae,

both feeding through pocket and occasional direct regurgitation were observed like as in the cells containing worker larvae.

It is said that the pollen is placed into the pollen pockets in pocket making species, whereas it is stored in empty cocoons in pollen storing species (Free & Butler, 1959). In the colonies of *B. diversus* observed, the workers never stored the pollen in storage receptacles other than pollen pockets. But Morimoto, Iwata and Yasumatsu (1951) recorded in the same species the deposition of a little quantity of pollen in 3 old cocoons used as receptacles. Tsuneki (1960) also observed in *B. diversus* the deposition of both pollen and nectar in old empty cocoons. In colony C, brood cell No. 37 was broken on Sept. 3, after the larvae in the cell died, and converted into the storage cylinder in which a small quantity of pollen was stored.

Summary

The present paper deals with the brood development and feeding habits in three colonies of *Bombus* (*Diversobombus*) *diversus* Smith kept in the artificial hives in Yaita City, Tochigi Pref., Japan. The results of observations are summarized as follows:

1) The duration of each developmental stage is as follows (in days): colony B: egg 4–5, larva 7–9, pupa (including prepupa) 10–12, total 22–24. colony C: egg 4–8 (mostly 4–6), larva 6–9 (mostly 6–8), pupa 10–12, total 20–25 (mostly 22–24).

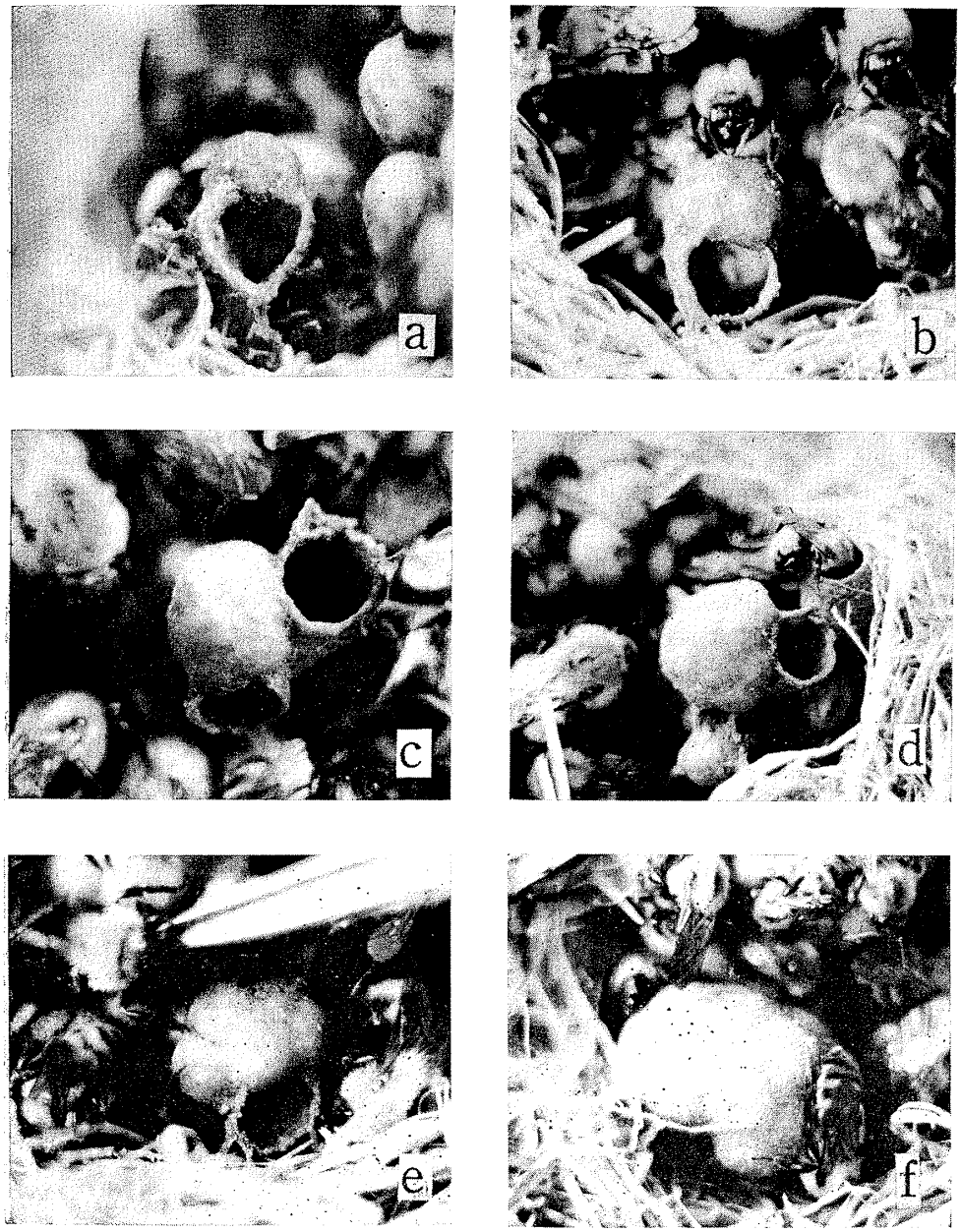
2) The workers construct the pollen pocket at one side of the brood cell soon after the hatching out of the larvae. In most cases 2 pockets are made in one cell. The pocket is usually removed in about 5 days after hatching out. The pocket changes its size parallel to the growth of the larvae (cf. Table 3).

3) Like as in other bumblebees the larvae dwell gregariously in the cell till cocoon spinning. The larval cells are 5–6.5 mm in diameter soon after hatching out and since 3 days after hatching out the position of each larva in the cell is detectable from outside of the cell as swellings. On 4 days after hatching out the larvae spin thin silken partition walls between themselves. The brood cell is dark brown soon after hatching out, becoming gradually paler and finally changes almost yellow just before cocoon spinning. The change of the size of cells is given in Table 4.

4) The duration of cocoon spinning is relatively constant, lasting mostly one day. The coloration of cocoons is at first bright or sulfur yellow with dark brown spots of wax not scratched off, later changing into dark brown on about 8–9 days after cocoon spinning. The cocoons developed from one egg-cell did not separate from one another, forming a group of cocoons.

5) The emergence from the same batch is relatively synchronous, taking 3 days for all adult bees. On emergence adult bees gnaw the wall of the cocoon from inside of the cocoon and other bees often help them to make the way out of the cocoon.

6) The pollen mass deposited into the pocket is kneaded with nectar and plastered to the pollen bed beneath the larvae by house bees. The larvae consume completely the pollen mass deposited into the pocket within about 5 days after hatching out. Thereafter, the remaining pollen mass is eaten by adult bees when they remove



Katayama—Brood development of *Bombus diversus*.

the pocket.

7) Adult bees occasionally feed both the worker and male larvae by means of the direct regurgitation through a hole made on the top of the cell which is closed soon after the regurgitation. In general the regurgitation is made only to the middle stage or older larvae of 4 to 5 days old, seldom to the younger ones.

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Explanation of Plate 1

Brood development of *Bombus diversus* Smith.

Fig. a: Brood cell No. 20 of one day old after hatching out.

Fig. b: Brood cell No. 26 of 2 days old after hatching out, white portion inside the pocket is pollen mass.

Fig. c: Brood cell No. 19 of 3 days old after hatching out, 2 pockets are constructed on one cell.

Fig. d: Brood cell No. 18 of 4 days old after hatching out.

Fig. e: Brood cell No. 24 of 5 days old after hatching out, the position of each larva in the cell is detectable from the outside of the cell as swellings.

Fig. f: Brood cell No. 25 of 6 days old after hatching out, the hollowed part under the cell is the vestige of the pocket already removed.

国際動物命名規約の邦訳

先年来，日本学術会議，動物学研究連絡委員会動物学命名法小委員会で邦訳を作製中であつた「第15回国際動物学会議において採用された，国際動物命名規約」1961年発行初版の訳書が出版されたので，入手希望の方は発行所北隆館に申し込まれたい．価格は 1,000 円であるが，本会会員であることを明らかにされれば，送料込み 900 円で入手できる．

（朝比奈正二郎）